22. Consumption and Diet Composition Matrix

Jason S. Link

Interaction Matrix - Fish

The standard Northeast Fisheries Science Center (NEFSC) bottom trawl survey program has been executed annually since 1963 (Grosslein 1969; Azarovitz 1981; NEFC 1988). During these surveys, food habits data are collected from a variety of species. These multi-species surveys were designed to monitor trends in abundance and distribution and to provide samples to study the ecology of the large number of fish and invertebrate species inhabiting the region. The surveys have generally utilized a 36' Yankee otter trawl towed at approximately 3.5 knots for 30 minutes at each station. Trawl stations were selected using a stratified random design. Within each stratum, stations were assigned randomly, and the number of stations allotted to a stratum was in proportion to its area. Station allotments were approximately one station per 200 square nautical miles. The surveys were conducted at depths of 27 m to 366 m; however, greater depths were occasionally sampled in the deep canyons along the continental shelf break. Once onboard, predators were sorted to species, weighed to the nearest 0.1 kg and measured to the nearest cm. Sex and maturity were determined, and subsamples of key species were eviscerated for feeding ecology studies.

The NEFSC has collected fish food habits data for over 30 years. Starting in 1973, individual stomach samples for selected species were preserved at sea in 10% buffered formalin for later prey identification. Individual stomach preservation was continued until 1981 for an expanding list of species. Prey weight (to 0.01 g), number, percent composition, total stomach weight (to 0.01 g), and lengths of fish prey (mm) were determined upon examination in the laboratory. Prey identification was to the lowest taxon feasible. In 1981 the stomachs of major species such as Atlantic cod, haddock, silver hake, yellowtail flounder, winter flounder, Atlantic herring, and Atlantic mackerel continued to be individually preserved, but prey of all other species were examined and identified at sea. In addition, a conversion from mass (g) to volumetric measurement of prey (to 0.1 cm^3) was initiated. Data on prey composition (%), numbers, and lengths were also collected shipboard. Since 1985, all stomach samples have been processed and prey identified at sea. To account for potential differences in the resolution of prey taxonomy between in-lab and at-sea sampling, we grouped most prey, particularly invertebrates, into broad prey categories (i.e., Class or Order). The exception was fish prey, which were maintained at the lowest feasible level. A conversion factor of 1.1 was used to convert prey volumes to weights based upon regression analyses (Link and Almeida 2000) similar to other studies (Bowman, unpublished manuscript; Tanasichuk *et al.* 1991; Garrison and Link 2000). For further details of the food habits data, see Link and Almeida (2000).

We estimated mean stomach contents (to 0.01 g) and diet composition (as a percentage of weight) for each EMAX predator node category by EMAX prey node category.

Interaction Matrix - Other Nodes

For those nodes for which we did not have direct diet information, we assumed that the values for each EMAX predator's diet composition fell within the range described for similar species in the literature. These percentages were adapted based on a suite of criteria (including suitability and known feeding patterns from local species of similar biology) so that each predator's diet summed to 100%. Examples of values can be found in the subject literature for each node or in food web compilations (e.g., Kenny *et al.* 1985, Overholtz *et al.* 1991, Pauly *et al.* 1995, Hammill *et al.* 1997, Kenny *et al.* 1997, Sigurjonsson and Vikingsson 1997, Stenson *et al.* 1997, Barros and Clarke 2002, Link 2002,). Values for the EMAX interaction matrix are in Table 22.1. We also show the connections for each node in Figure 22.1.

Fish Consumption

We calculated the percent composition by weight of each major EMAX prey category in relation to the total amount consumed by each EMAX fish predator. Using a two-stage cluster method we weighted these values by the number of tows and the number of fish in a tow (see equations below). Link and Almeida (2000) provide a more thorough discussion of the statistics behind these methods and their calculation.

Based on an evacuation rate model (Eggers 1977; Elliot and Persson 1978), daily consumption estimates (C_d) were calculated for an average predator in each of the EMAX fish groups as

(EQ. 22.1)
$$C_{d_i} = 24 \cdot E_i \cdot \bar{S}_i^{\gamma},$$

where 24 is the number of hours in a day, *i* is the species of fish, γ is a constant (usually assumed to be equal to 1). The evacuation rate *E* is

(EQ. 22.2)
$$E_i = \alpha e^{\beta T_p},$$

where α and β are both fitted constants and T is temperature. Based on literature values and sensitivity analyses, we set α and β to 0.004 and 0.115, respectively (Durbin *et al.* 1983; Overholtz *et al.* 1999). We used a mean temperature for two (approximately semiannual) time periods (*p*) per year: 1) winter and spring surveys combined, and 2) summer and fall surveys combined (D. Mountain and M. Taylor; NEFSC, Woods Hole, Massachusetts, unpublished data).

From Equation 22.1 above, $\bar{S}_i$ is the mean total stomach contents (g), such that

(EQ. 22.3)
$$\bar{S}_i = \frac{\sum_{t=1}^{n_t} n_{it} \cdot \bar{S}_{it}}{n_t},$$

where n_t is the number of tows for all strata sampled, n_{it} is the number of predator stomachs within a tow, and

(EQ. 22.4)
$$\bar{S}_{it} = \frac{\sum_{k=1}^{n_{it}} S_{itk}}{n_{it}}$$

is the mean stomach weight of predator *i* in tow *t*, where *k* represents an individual fish.

The daily consumption rates from both semiannual time periods were combined into a total, annual population level consumption rate (*C*):

$$C_i = \sum_{1}^{p} (C_{d_i} \cdot d_p) \quad \text{(EQ. 22.5)},$$

where d is the number of days in each time period p (182.5 for each, corresponding to the bottom trawl survey; NEFSC 1998).

The total amount of a particular EMAX prey (j) consumed by an EMAX fish predator (i), (C_{ij}), was estimated by multiplying the total consumption (Equation 5) by the (fixed) percentage (D_{ij}) of each prey comprising the diets of these predators, such that

$$C_{ij} = C_i \cdot D_{ij} \quad \text{(EQ. 22.6)},$$

where D_{ij} is

$$D_{ij} = \frac{\overline{S}_{ij}}{\overline{S}_i} \quad \text{(EQ. 22.7)},$$

and where $\overline{S_i}$ is from equation 3 and $\overline{S_{ij}}$ is

$$\overline{S}_{ij} = \frac{\sum_{t=1}^{n_t} n_{it} \cdot \overline{S}_{ijt}}{n_t} \quad \text{(EQ. 22.8)},$$

where

$$\overline{S}_{ijt} = \frac{\sum_{k=1}^{n_{it}} S_{ijtk}}{n_{it}} \quad \text{(EQ. 22.9)}.$$

Given the short time span of the project, we chose to use a fixed diet composition for the EMAX prey (D_{ij}). All other parameters were estimated for two periods each year and the annual consumption was allocated according to the fixed diet proportion, D_{ij}. We examined the mean, minimum, and maximum consumption estimates to ascertain the range of possible EMAX prey removals by these fish predators.

It was determined that we needed a per capita consumption rate for each EMAX fish predator. Thus, the factor in Equation 22.5 was adopted and integrated across a year to give an annual average without scaling to population abundance.

The average sizes (weight) of the EMAX fish predators were then calculated to give an estimate of per capita biomass, B_i. The annual estimate of consumption, C_i, was then used with the estimate of average biomass, B_i, to calculate the C:B ratio.

These estimates were calculated for the following nodes:

Small Pelagics - commercial
Small Pelagics - other
Small Pelagics - squid

Small Pelagics - anadromous
Medium Pelagics - (piscivores and other)
Demersals - benthivores
Demersals - omnivores
Demersals – piscivores

For examples of where this approach has been previously used see Link *et al.* (2002), Link and Garrison (2002), and Overholtz *et al.* (1999, 2000).

For all other EMAX nodes, literature values of C:B were used to estimate consumption. Further details are given in sections in this volume specific to each group.

Integrating Consumptive Removals

For each EMAX node, the total consumption was multiplied by the diet composition vector (Equation 22.6) to allocate the amount removed via consumption by each predator node for all EMAX prey nodes. These vectors were then summed across the cross-vector (or row) for each prey item to calculate a total amount of biomass removed per year for each EMAX node.

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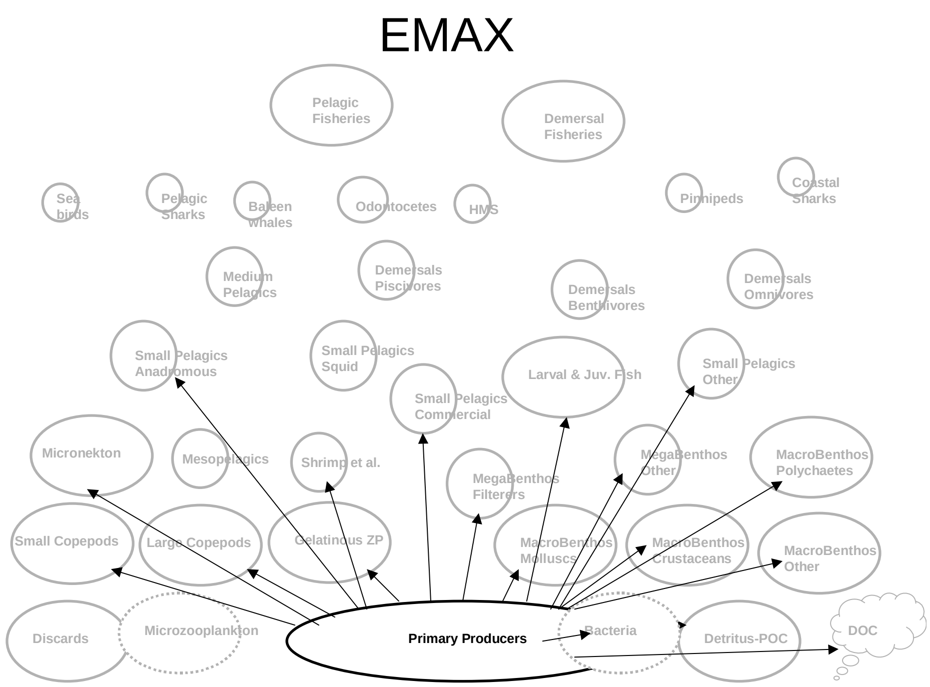
Table 22.1. Example EMAX interaction matrix for GOM. Flows are from row to column.

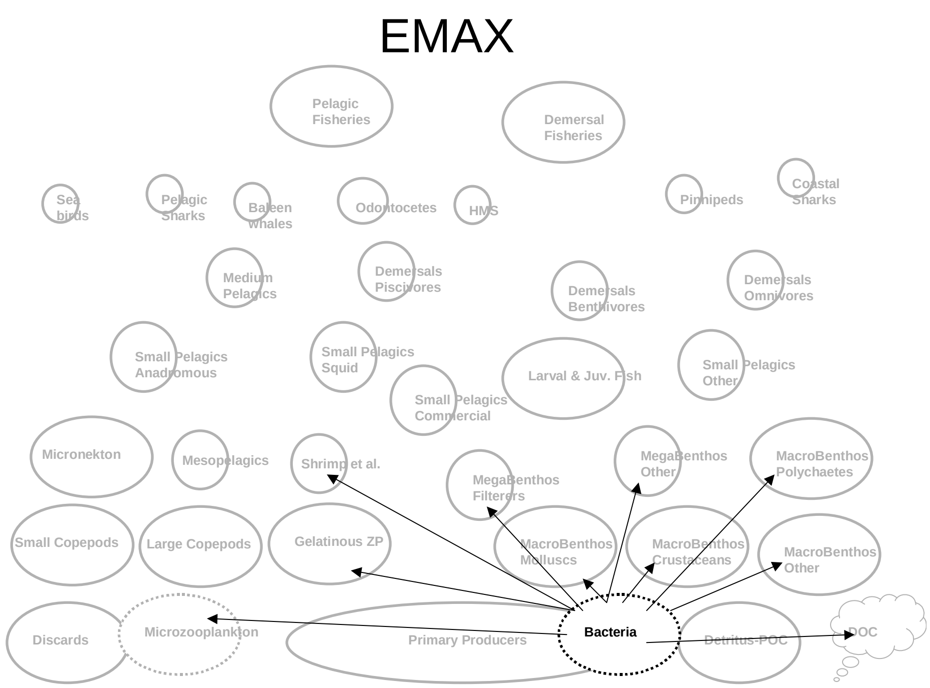
	Phytoplankton - Primary Producers	Bacteria	Microzooplankton	Small Copepods	Large Copepods	Gelatinous Zooplankton	Micronekton	Macrobenthos - polychaetes	Macrobenthos - crustaceans	Macrobenthos - molluscs	Macrobenthos - other	Megabenthos - filterers	Megabenthos - other	Shrimp *et al.*
Phytoplankton - Primary Producers	0	15	15	61	46	8.6	11.4	10.8	12.0	37.9	14.9	60	0	5.4
Bacteria	0	0	40	0	0	2	0	26.0	10.6	17.5	16.0	20	12	32
Microzooplankton	0	0	10	20	5	5	0	0	0	0	0	0	0	0
Small Copepods	0	0	0	8	28	33	51.3	0	1.1	0	0	0	0	0
Large Copepods	0	0	0	0	10.3	36	22.9	0	2.1	0	0	0	0	0
Gelatinous Zooplankton	0	0	0	0	5	2.1	0	0	0	0	0	0	0	0
Micronekton	0	0	0	0	0	0	2.9	0	0	0	0	0	0	10.8
Macrobenthos - polychaetes	0	0	0	0	0	0	0	9.4	10.0	0	5.0	0	6.7	0
Macrobenthos - crustaceans	0	0	0	0	0.3	0	0	1.7	10.4	0	5.0	0	6.7	5.4
Macrobenthos - molluscs	0	0	0	0	0	0	0	0.9	14.2	6.7	14.9	0	20.1	0
Macrobenthos - other	0	0	0	0	0.4	0	0	5.1	10.4	5.2	8.0	0	20.1	7.5
Megabenthos - filterers	0	0	0	0	0	0	0	0.3	1.1	1.1	0.4	0	3.3	0
Megabenthos - other	0	0	0	0	0	0	0	0.33	1.0	1.1	5.0	0	14.3	0
Shrimp *et al.*	0	0	0	0	0	0	0	0	0	0	0	0	0	1.5
Larval and Juvenile Fish - all	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Small Pelagics - commercial	0	0	0	0	0	1.5	0	0	0	0	0	0	0	0
Small Pelagics - other	0	0	0	0	0	0.4	0	0	0	0	0	0	0	0
Small Pelagics - squid	0	0	0	0	0	0.3	0	0	0	0	0	0	0	0
Small Pelagics - anadromous	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0
Medium Pelagics - piscivores & other	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Demersals - benthivores	0	0	0	0	0	0	0	0	0.4	0	0.5	0	0.7	0
Demersals - omnivores	0	0	0	0	0	0	0	0	0.2	0	0.3	0	0.4	0
Demersals - piscivores	0	0	0	0	0	0	0	0	0	0	0.3	0	0.4	0
Sharks - coastal	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Highly Migratory Species	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pinnipeds	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Baleen Whales	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Odontocetes	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sea Birds	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Discards	0	0	0	0	0	0	0	0.5	0.5	0.5	0.7	0	3.3	5.4
Detritus - POC	0	85	35	11	5	10	11.5	45	26	30	29	20	12	32

Table 21.1, continued.

	Small Pelagics - commercial	Small Pelagics - other	Small Pelagics - squid	Small Pelagics - anadromous	Medium Pelagics - piscivores & other	Demersals - benthivores	Demersals - omnivores	Demersals - piscivores	Sharks - pelagics	Highly Migratory Species	Pinnipeds	Baleen Whales	Odontocetes	Sea Birds
Phytoplankton - Primary Producers	1.1	15.7	0	1.1	0	0	0	0	0	0	0	0	0	0
Bacteria	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Microzooplankton	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Small Copepods	11.7	11.5	0	7.9	0	0	0	0	0	0	0	5.8	0	0
Large Copepods	42.6	64.1	9	87.4	0	0	0	0	3	0	0	46.2	0	3
Gelatinous Zooplankton	2.1	3.1	0	0	0.1	0.5	1.2	0.1	0	7.2	0	0.1	0.3	0
Micronekton	21.3	4.2	45	1.9	0	6.1	3.5	2.2	0	0	7.4	28.9	2.5	12.3
Macrobenthos - polychaetes	1.1	0	0	0.3	0	14.6	17.7	1.1	0	0	0	0	0	0
Macrobenthos - crustaceans	6.7	0.2	13.5	0.6	1.2	18.1	17.7	1.1	1	0	0	5.8	0	0
Macrobenthos - molluscs	1.1	0.2	0	0	0	12.2	17.7	3.3	0	0	0	1.2	0	0
Macrobenthos - other	1.1	0.3	1.5	0	1.2	18.0	11.8	10.9	1	0	0	2.3	0	0
Megabenthos - filterers	0	0	0	0	0	5.2	4.3	1.1	0	0	0	0	0	0
Megabenthos - other	0	0	0	0	19	9.5	11.8	2.2	0	0	0	0.7	0	0
Shrimp *et al.*	0	0	6.8	0	2.4	2.1	0.4	15.3	0	0	0	0	0	6.2
Larval and Juvenile Fish - all	10.6	0.7	15	0.8	1.2	0	1.2	1.1	0	0	0	0	0	0
Small Pelagics - commercial	0	0	1.4	0	35.5	6	5.8	27	21	14.4	44.5	5.8	35.2	27.3
Small Pelagics - other	0	0	1.5	0	3.6	0.2	0.2	5.6	5	72.1	14.8	0.6	19	23.5
Small Pelagics - squid	0	0	6.1	0	3.6	0.4	0.2	5.5	16	6.3	0	1.1	25.4	6.1
Small Pelagics - anadromous	0	0	0.2	0	2.4	0	0	0.2	2	0	11	0.3	4.6	4
Medium Pelagics - piscivores & other	0	0	0	0	0.1	0	0	0	13	0	0.1	0	0.1	0.1
Demersals - benthivores	0.2	0	0	0	11.9	3.7	1.3	1.1	5	0	7.4	0	0	0
Demersals - omnivores	0.2	0	0	0	5.9	0.6	1	0.4	8	0	7.4	0	6.3	3.7
Demersals - piscivores	0.2	0	0	0	11.9	0.4	0.6	21.8	7	0	7.4	0	6.3	2.5
Sharks - coastal	0	0	0	0	0	0	0	0	3	0	0	0	0	0
Highly Migratory Species	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Pinnipeds	0	0	0	0	0	0	0	0	3	0	0	0	0	0
Baleen Whales	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Odontocetes	0	0	0	0	0	0	0	0	2	0	0	0	0.3	0
Sea Birds	0	0	0	0	0	0	0	0	3	0	0	0	0	0
Discards	0	0	0	0	0	1.2	2.4	0		0	0	0	0	11.3
Detritus - POC	0	0	0	0	0	1.2	1.2	0	5	0	0	1.2	0	0

Figure 22.1. Network connections for each node, showing the flows from one node to its consumer nodes.





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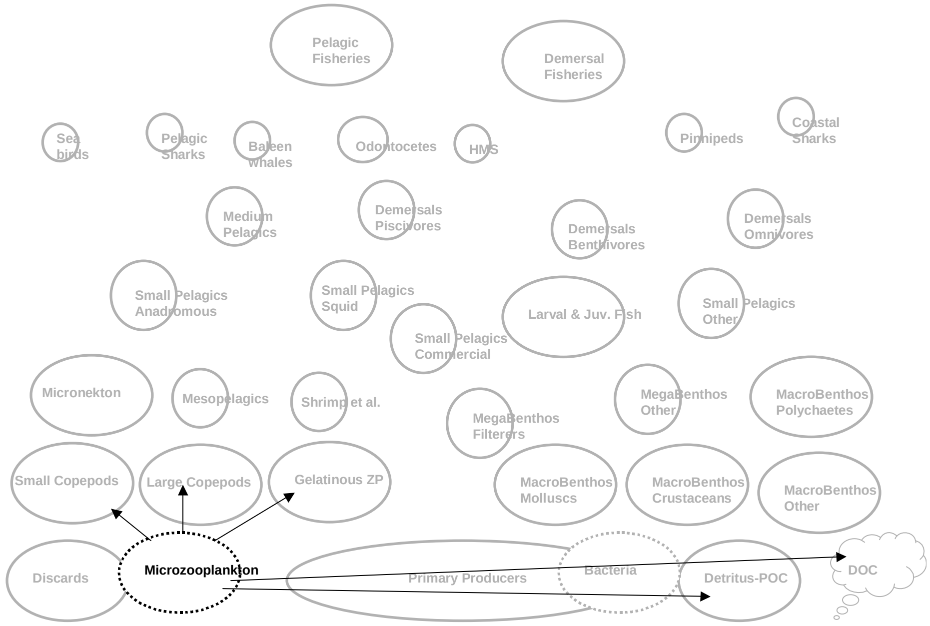
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Demersal Fisheries
Sea birds
Pelagic Sharks
Baleen whales
Odontocetes
HMS
Pinnipeds
Coastal Sharks
Medium Pelagics
Demersals Piscivores
Demersals Benthivores
Demersals Omnivores
Small Pelagics Anadromous
Small Pelagics Squid
Small Pelagics Commercial
Larval & Juv. Fish
Small Pelagics Other
Micronekton
Mesopelagics
Shrimp et al.
MegaBenthos Filterers
MegaBenthos Other
MacroBenthos Polychaetes
Small Copepods
Large Copepods
Gelatinous ZP
MacroBenthos Molluscs
MacroBenthos Crustaceans
MacroBenthos Other
Discards
Microzooplankton
Primary Producers
Bacteria
Detritus-POC
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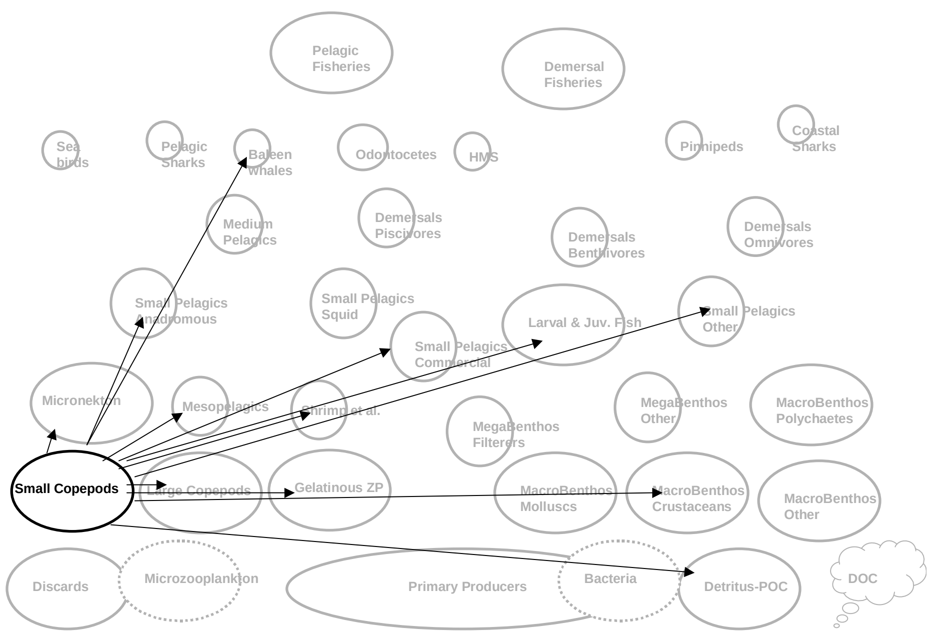
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Sea birds
Pelagic Sharks
Baleen whales
Odontocetes
HMS
Pinnipeds
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Demersals Benthivores
Demersals Omnivores
Small Pelagics Anadromous
Small Pelagics Squid
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Shrimp et al.
MegaBenthos Filterers
MegaBenthos Other
MacroBenthos Polychaetes
Small Copepods
Large Copepods
Gelatinous ZP
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Detritus-POC
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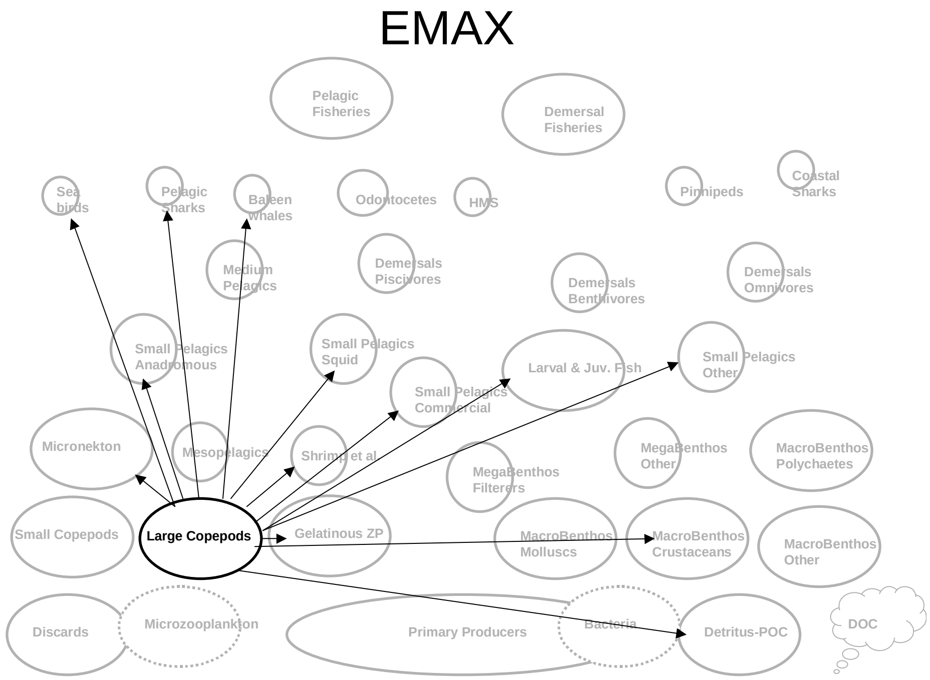
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Sea birds
Pelagic Sharks
Baleen whales
Odontocetes
HMS
Pinnipeds
Coastal Sharks
Medium Pelagics
Demersals Piscivores
Demersals Benthivores
Demersals Omnivores
Small Pelagics Anadromous
Small Pelagics Squid
Small Pelagics Commercial
Larval & Juv. Fish
Small Pelagics Other
Micronekton
Mesopelagics
Shrimp et al.
MegaBenthos Filterers
MegaBenthos Other
MacroBenthos Polychaetes
Small Copepods
Large Copepods
Gelatinous ZP
MacroBenthos Molluscs
MacroBenthos Crustaceans
MacroBenthos Other
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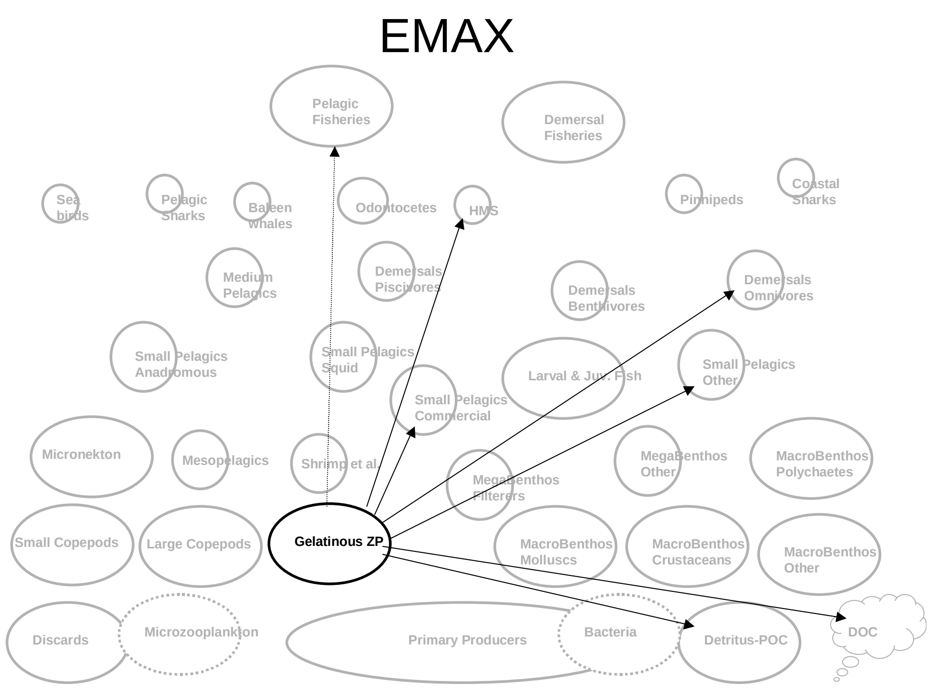
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Sea birds
Pelagic Sharks
Baleen whales
Odontocetes
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Pinnipeds
Coastal Sharks
Medium Pelagics
Demersals Piscivores
Demersals Benthivores
Demersals Omnivores
Small Pelagics Anadromous
Small Pelagics Squid
Small Pelagics Commercial
Larval & Juv. Fish
Small Pelagics Other
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Mesopelagics
Shrimp et al.
MegaBenthos Filterers
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MacroBenthos Polychaetes
Small Copepods
Large Copepods
Gelatinous ZP
MacroBenthos Molluscs
MacroBenthos Crustaceans
MacroBenthos Other
Discards
Microzooplankton
Primary Producers
Bacteria
Detritus-POC
DOC

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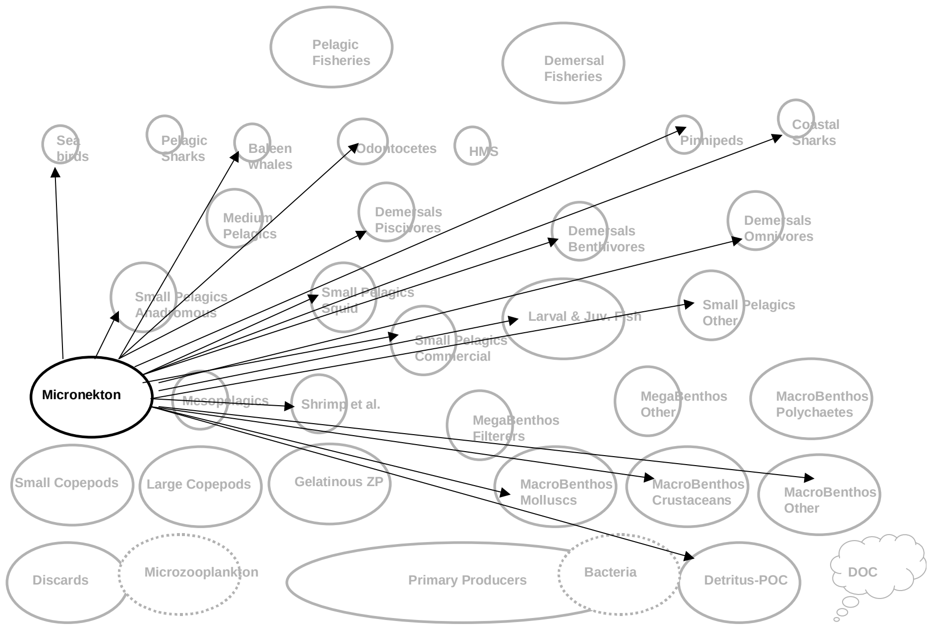
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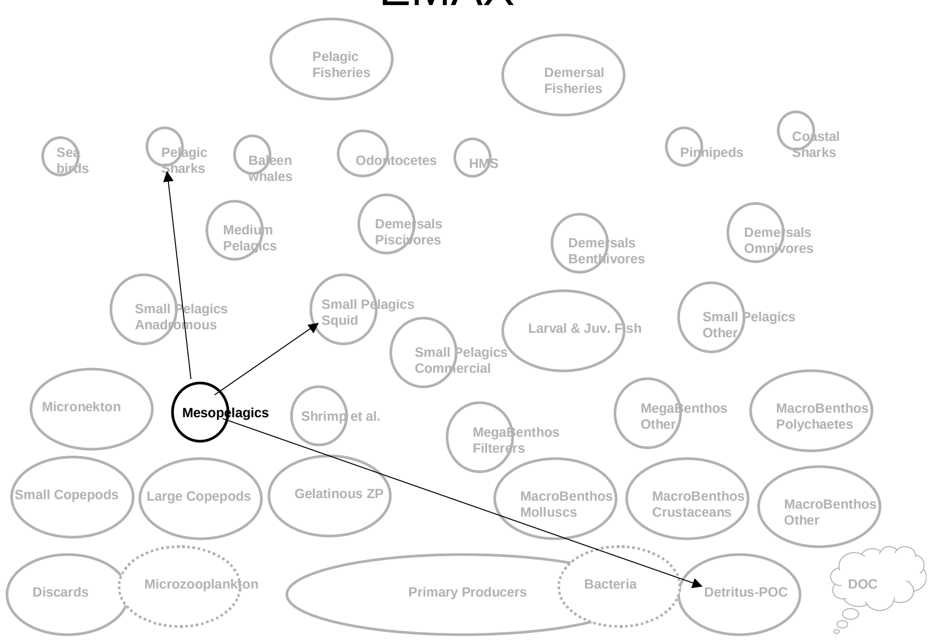
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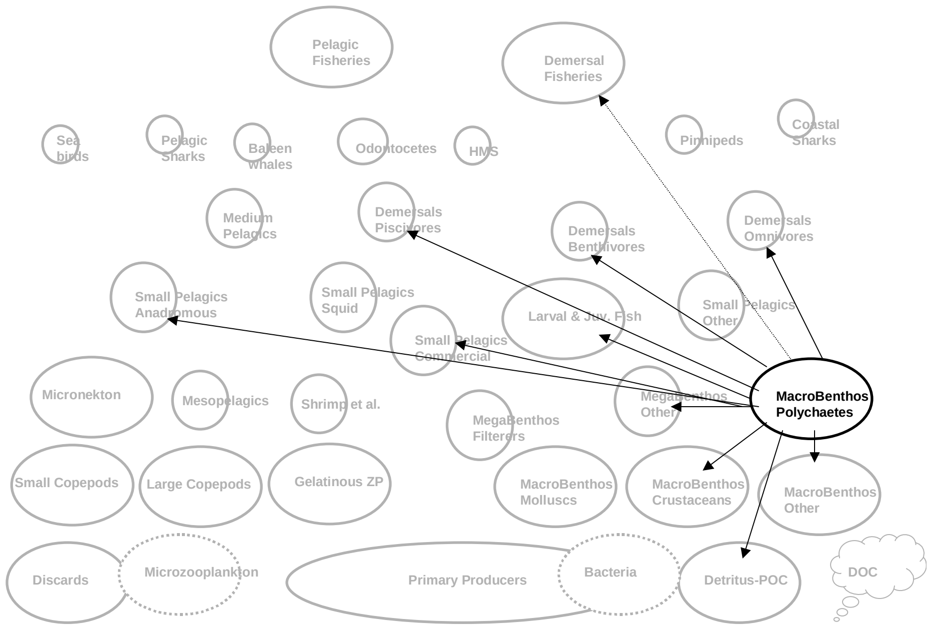

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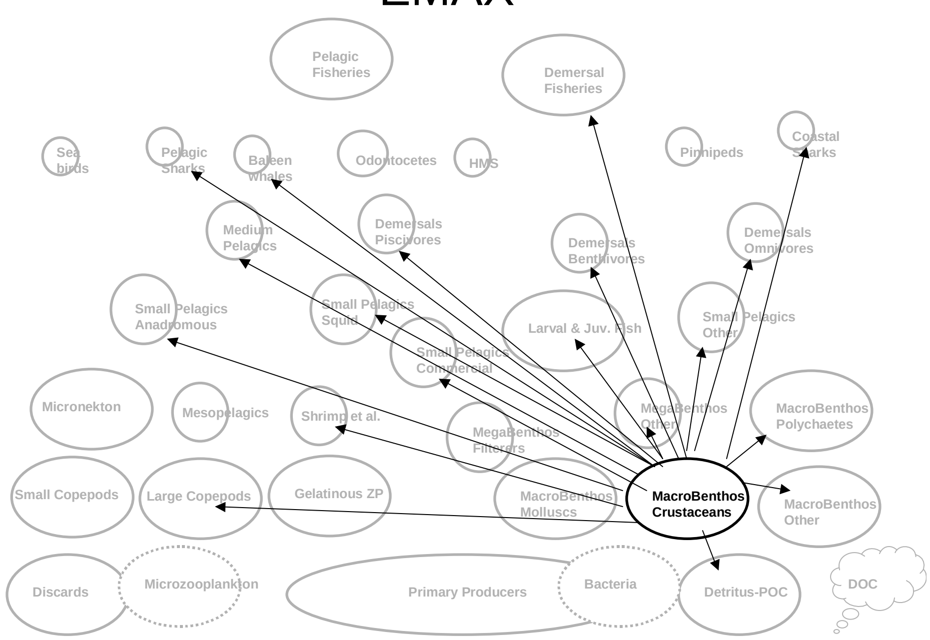

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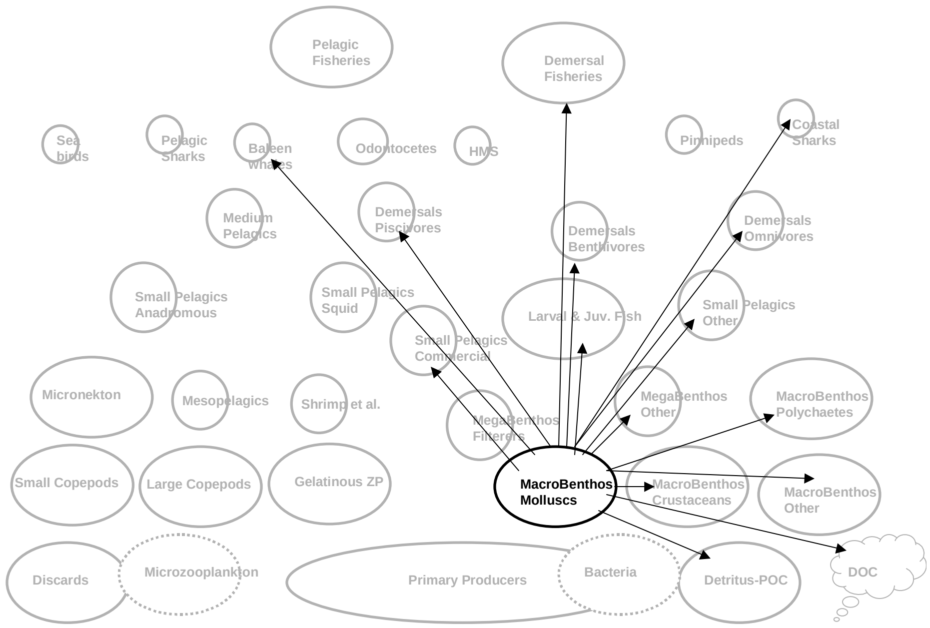

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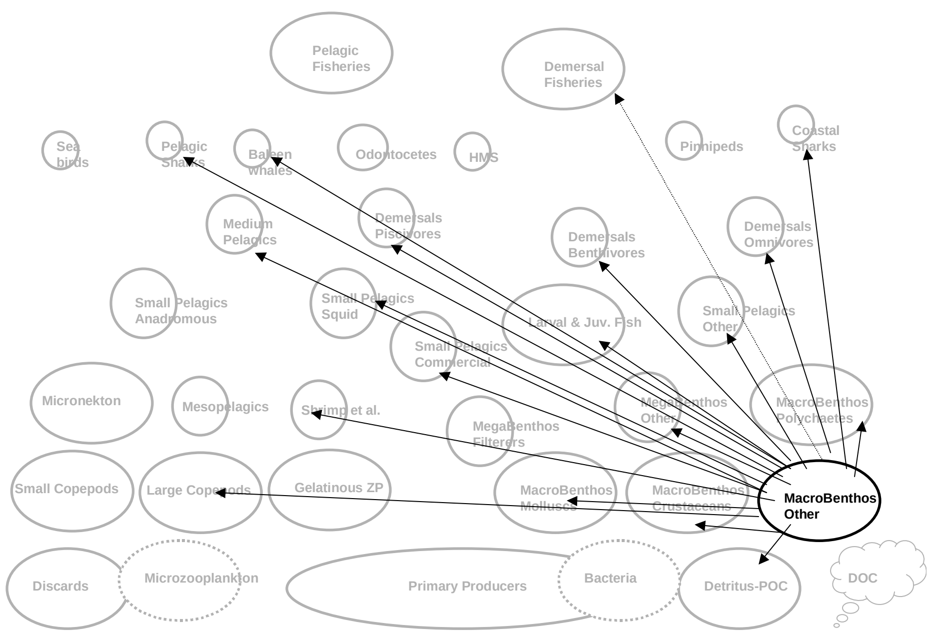

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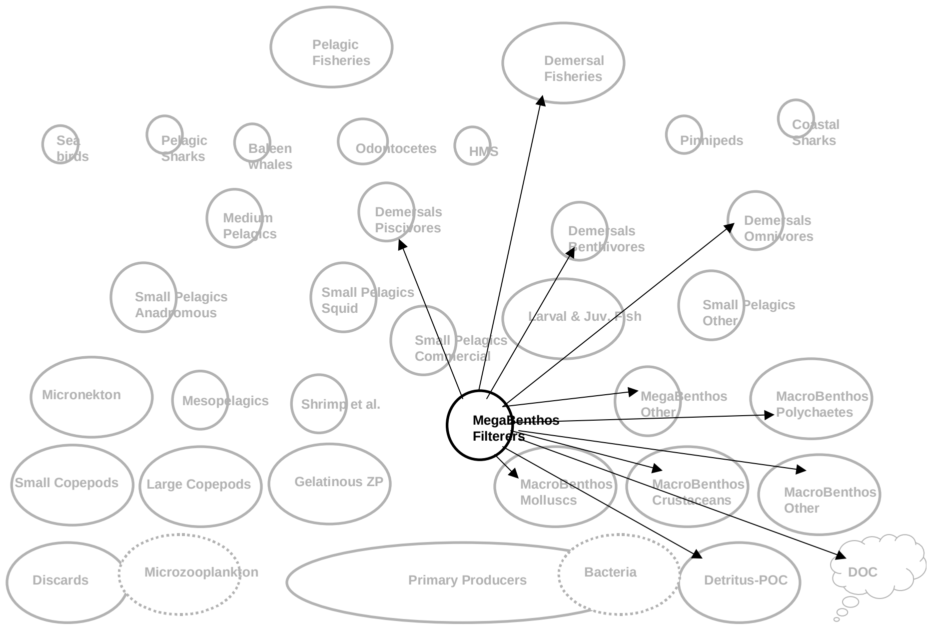

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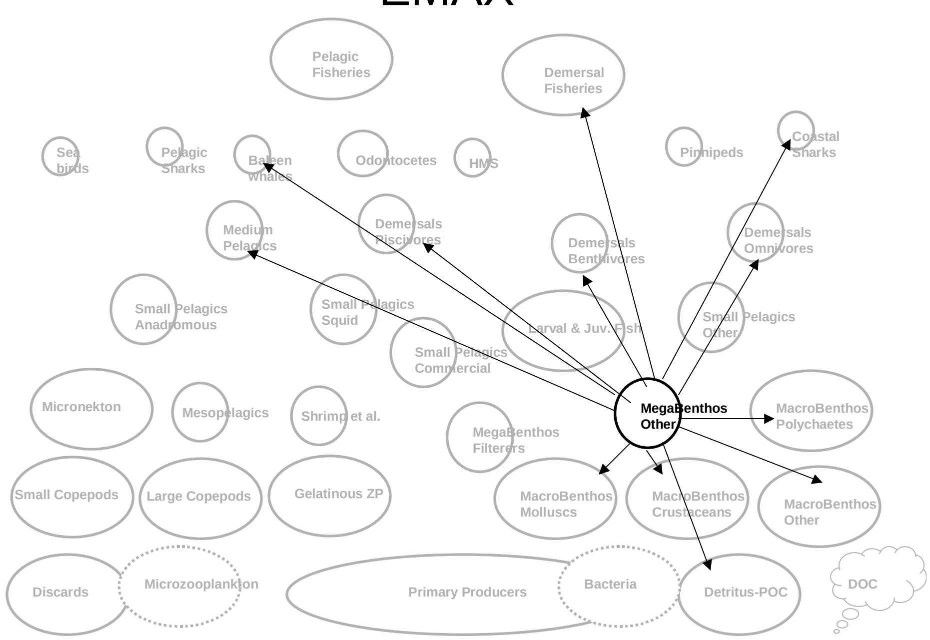

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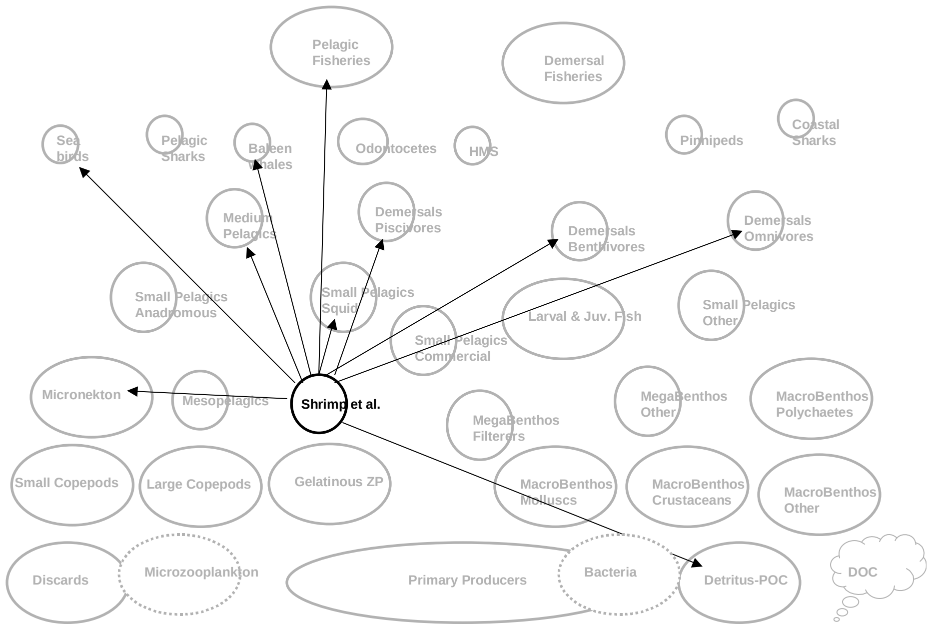
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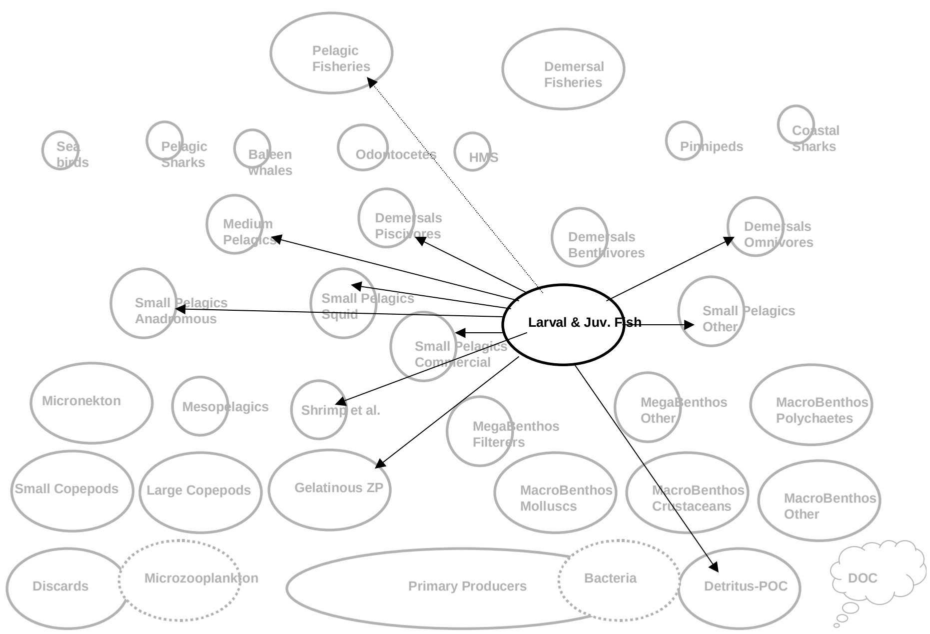
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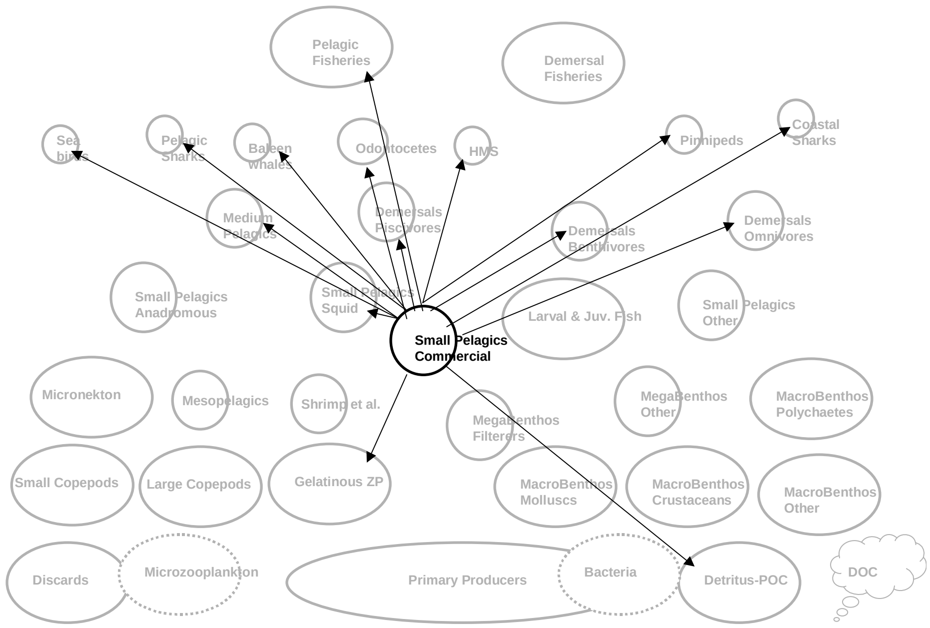
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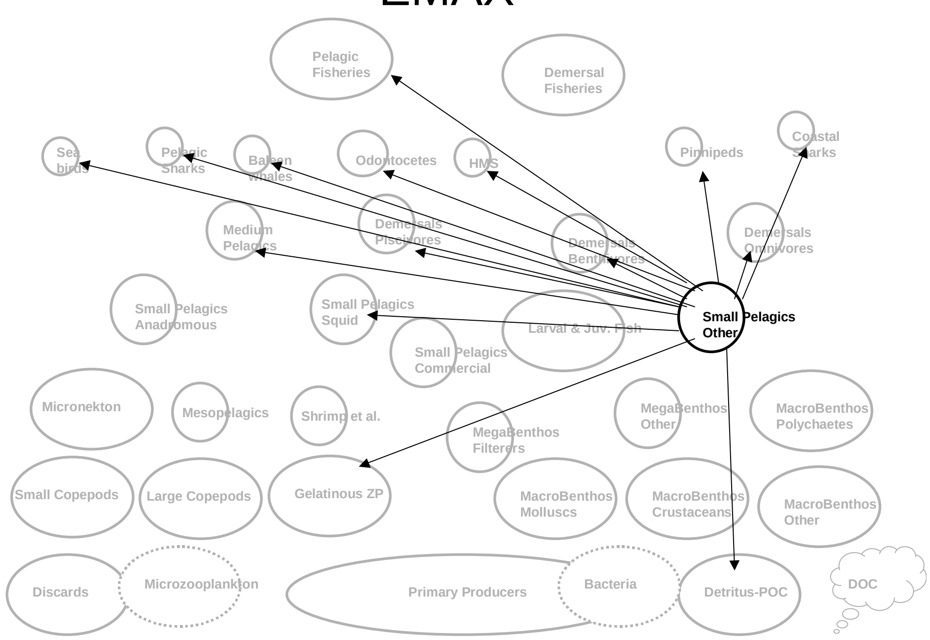
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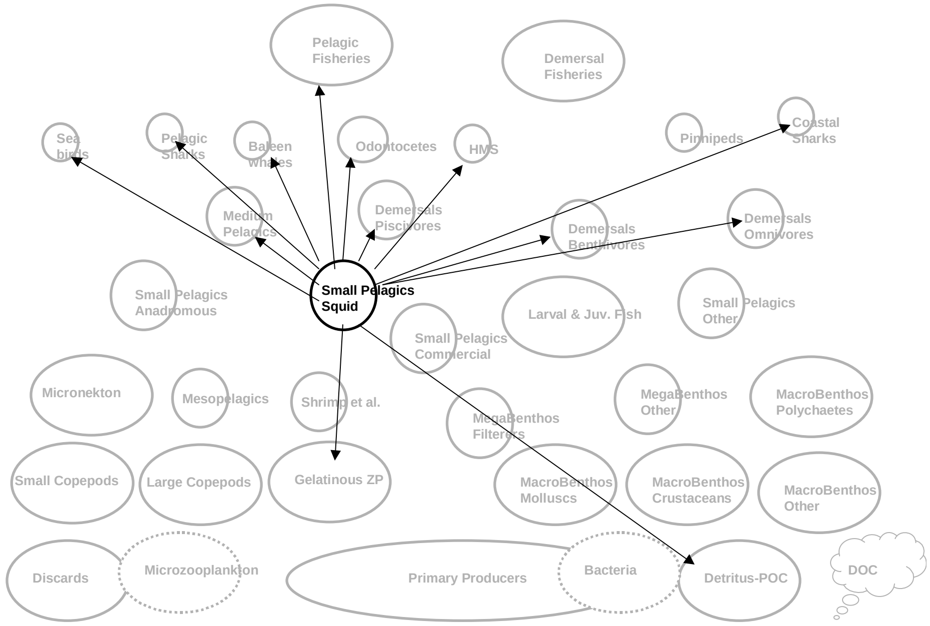
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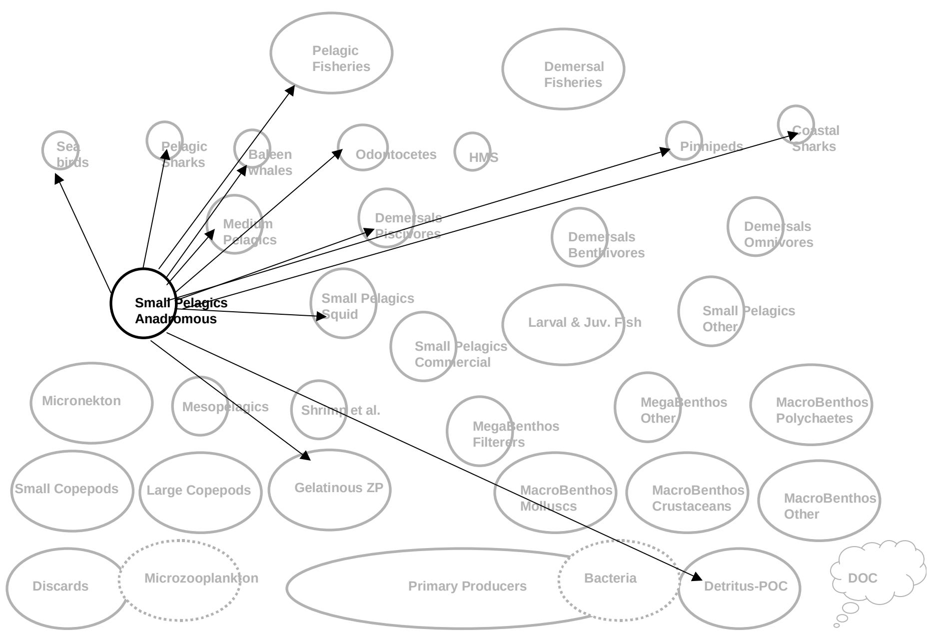
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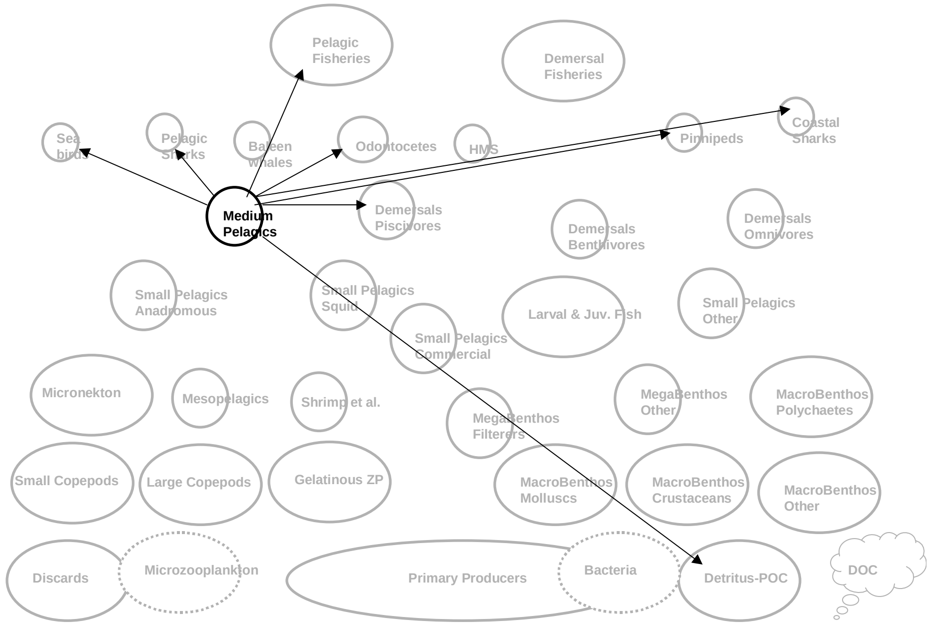
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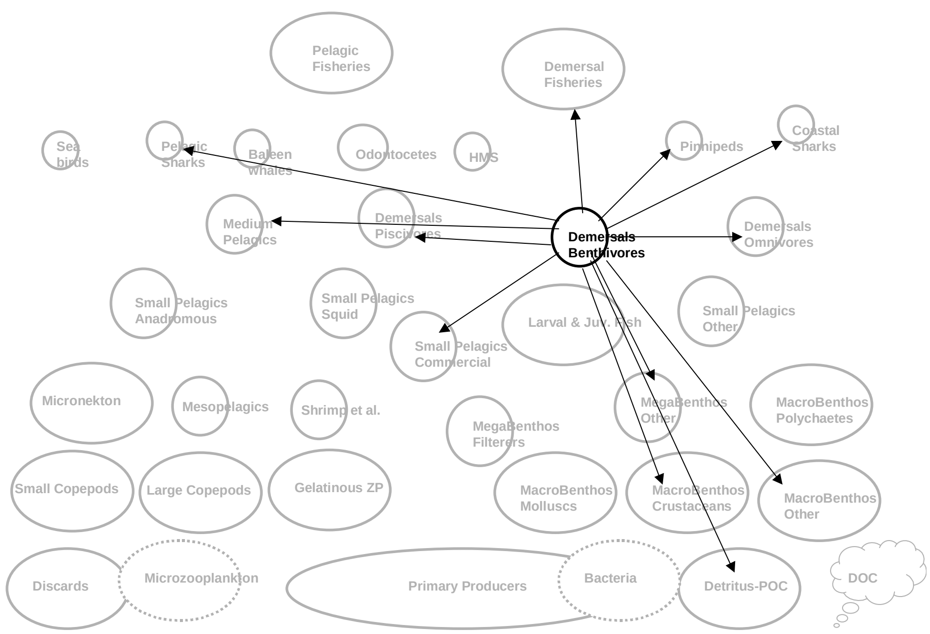
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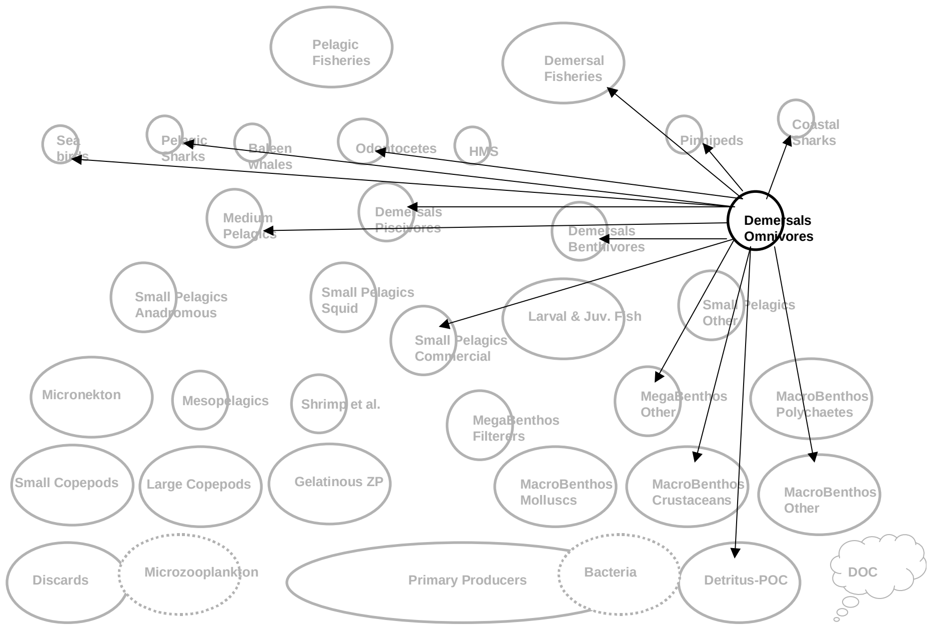

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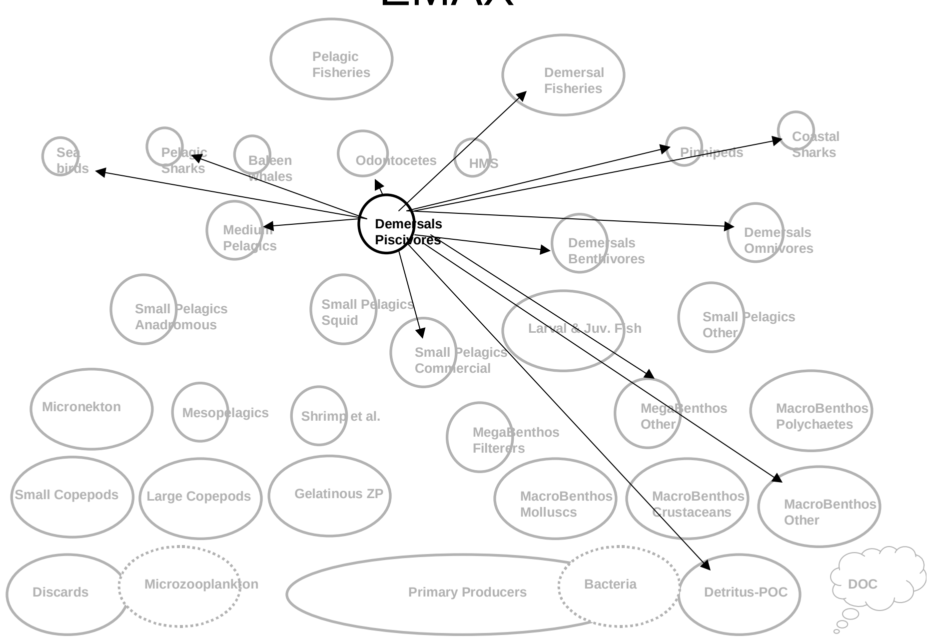

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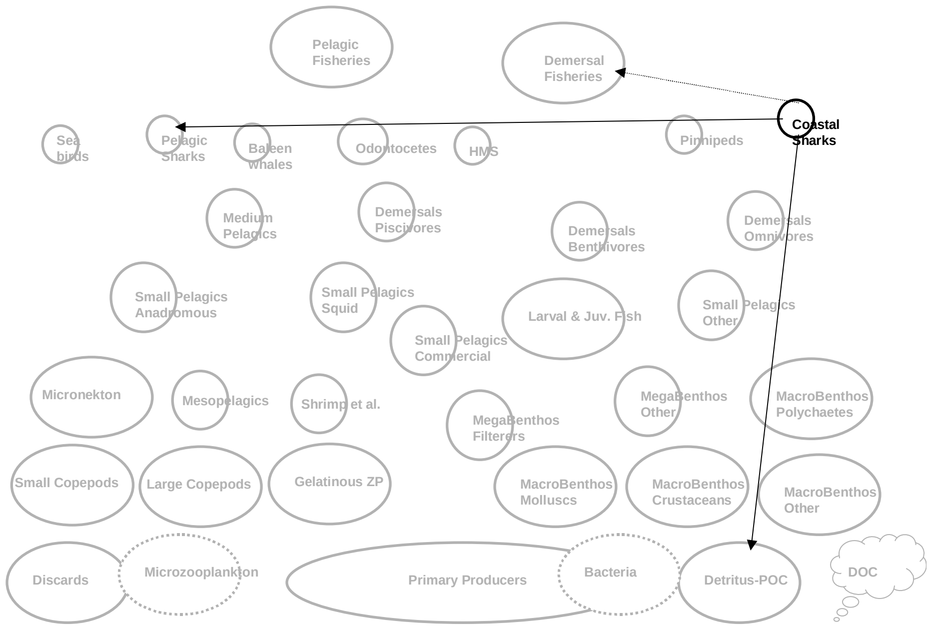
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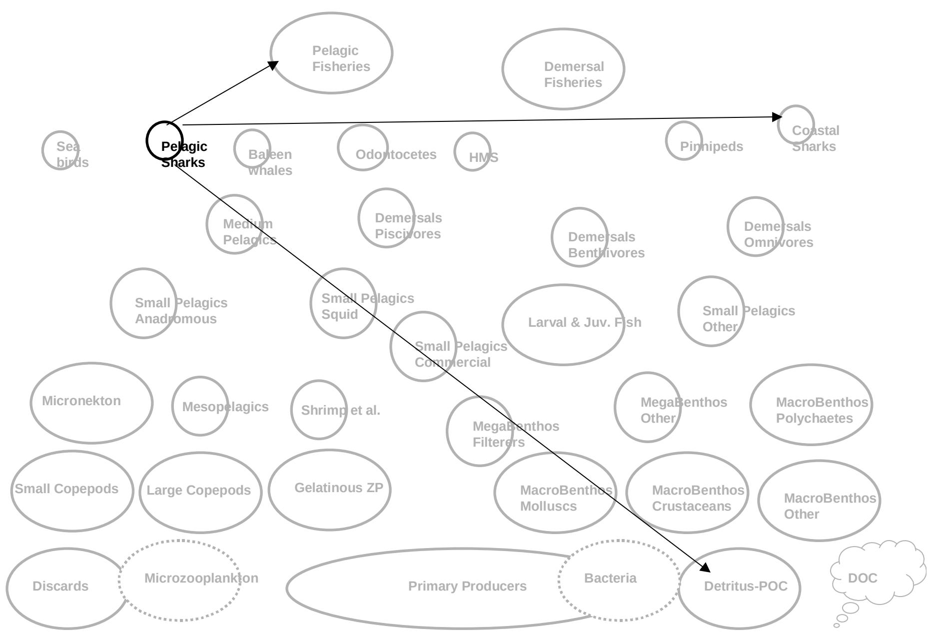
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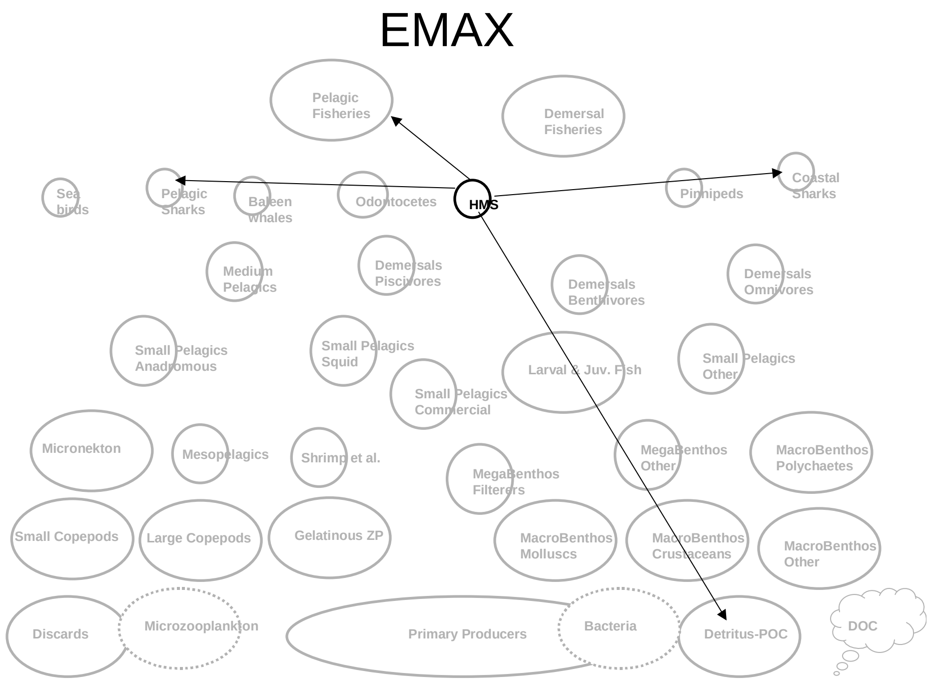
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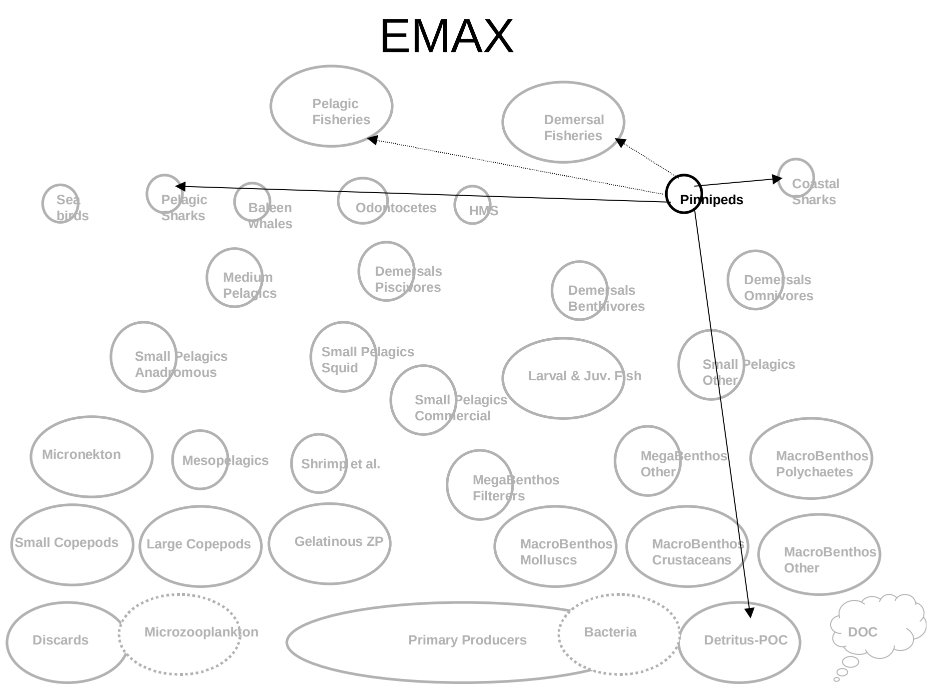
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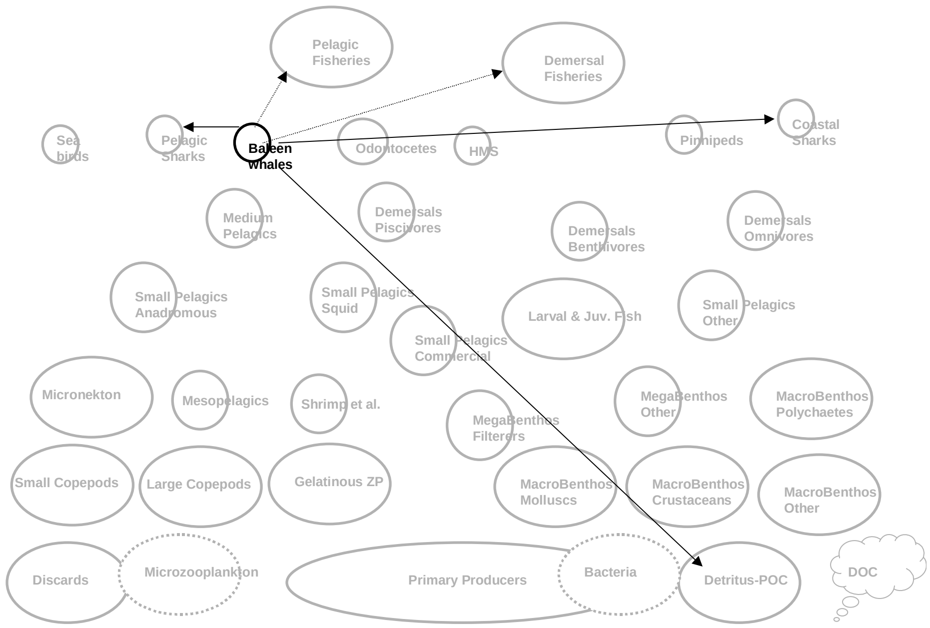
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Demersal Fisheries
Sea birds
Pelagic Sharks
Baleen whales
Odontocetes
HMS
Pinnipeds
Coastal Sharks
Medium Pelagics
Demersals Piscivores
Demersals Benthivores
Demersals Omnivores
Small Pelagics Anadromous
Small Pelagics Squid
Small Pelagics Commercial
Larval & Juv. Fish
Small Pelagics Other
Micronekton
Mesopelagics
Shrimp et al.
MegaBenthos Filterers
MegaBenthos Other
MacroBenthos Polychaetes
Small Copepods
Large Copepods
Gelatinous ZP
MacroBenthos Molluscs
MacroBenthos Crustaceans
MacroBenthos Other
Discards
Microzooplankton
Primary Producers
Bacteria
Detritus-POC
DOC

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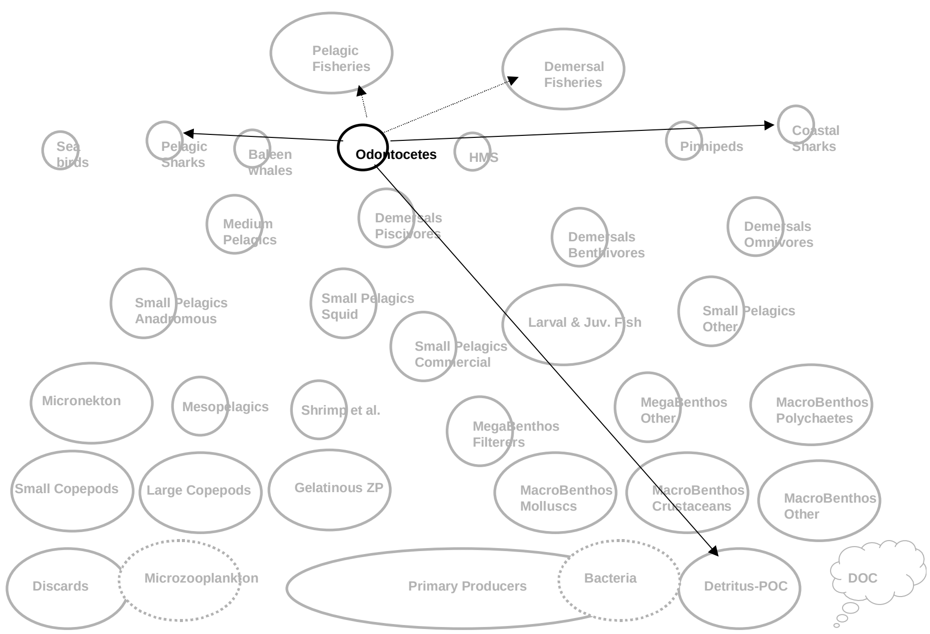
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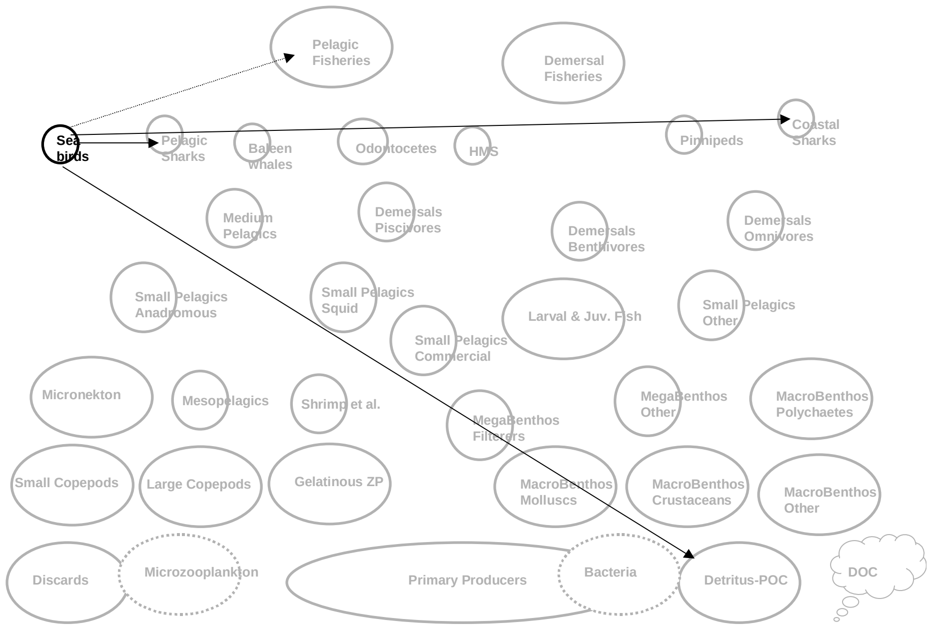
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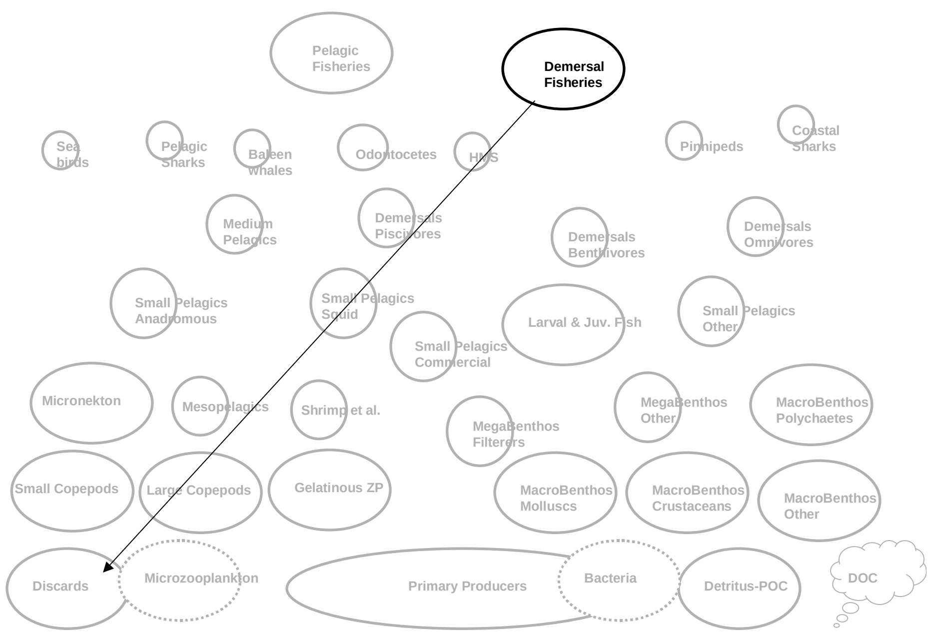
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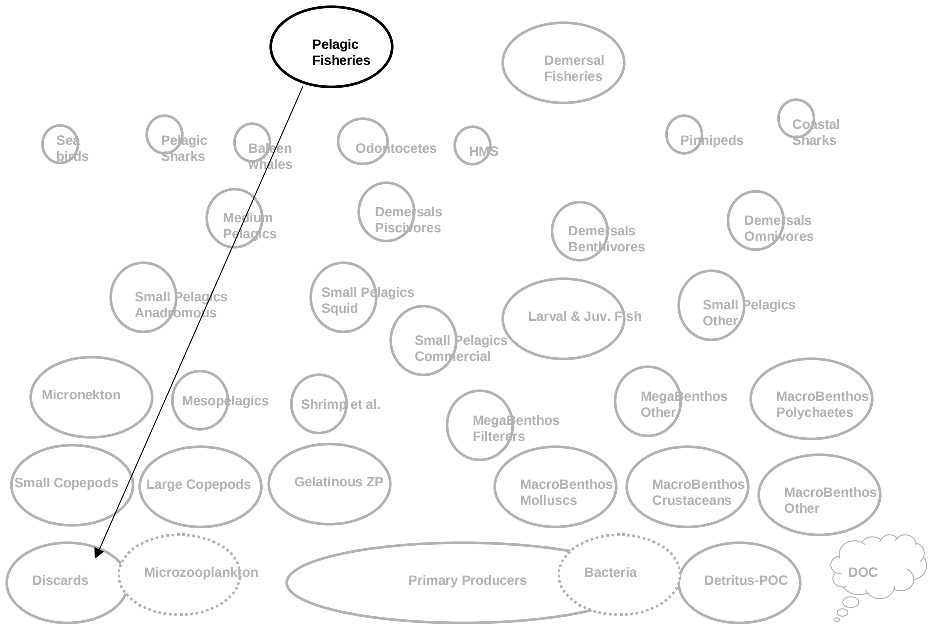
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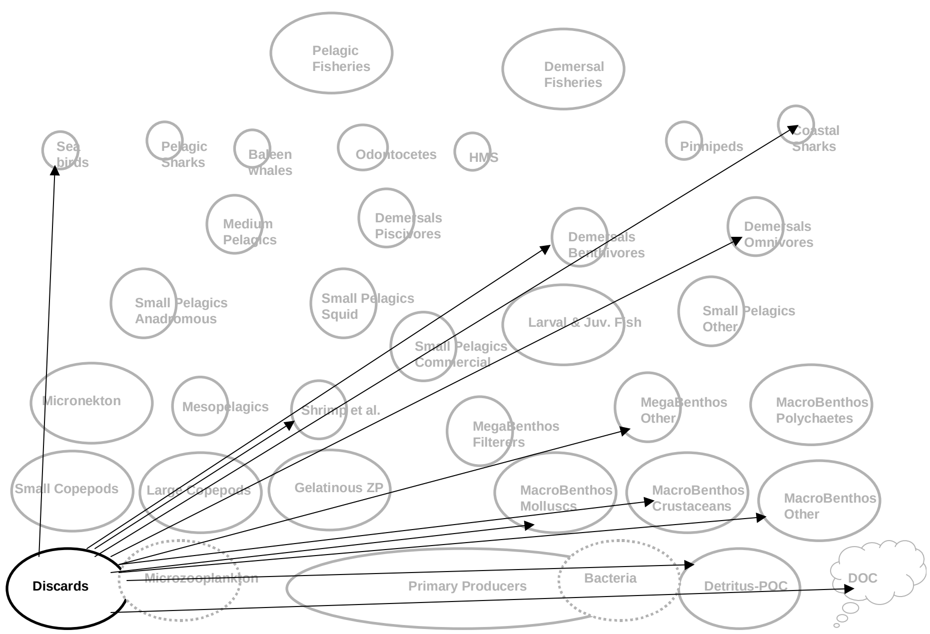
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